Working Conceptual Model for the Food Web of the San Francisco Bay/Delta Estuary — Interagency Technical Report 42

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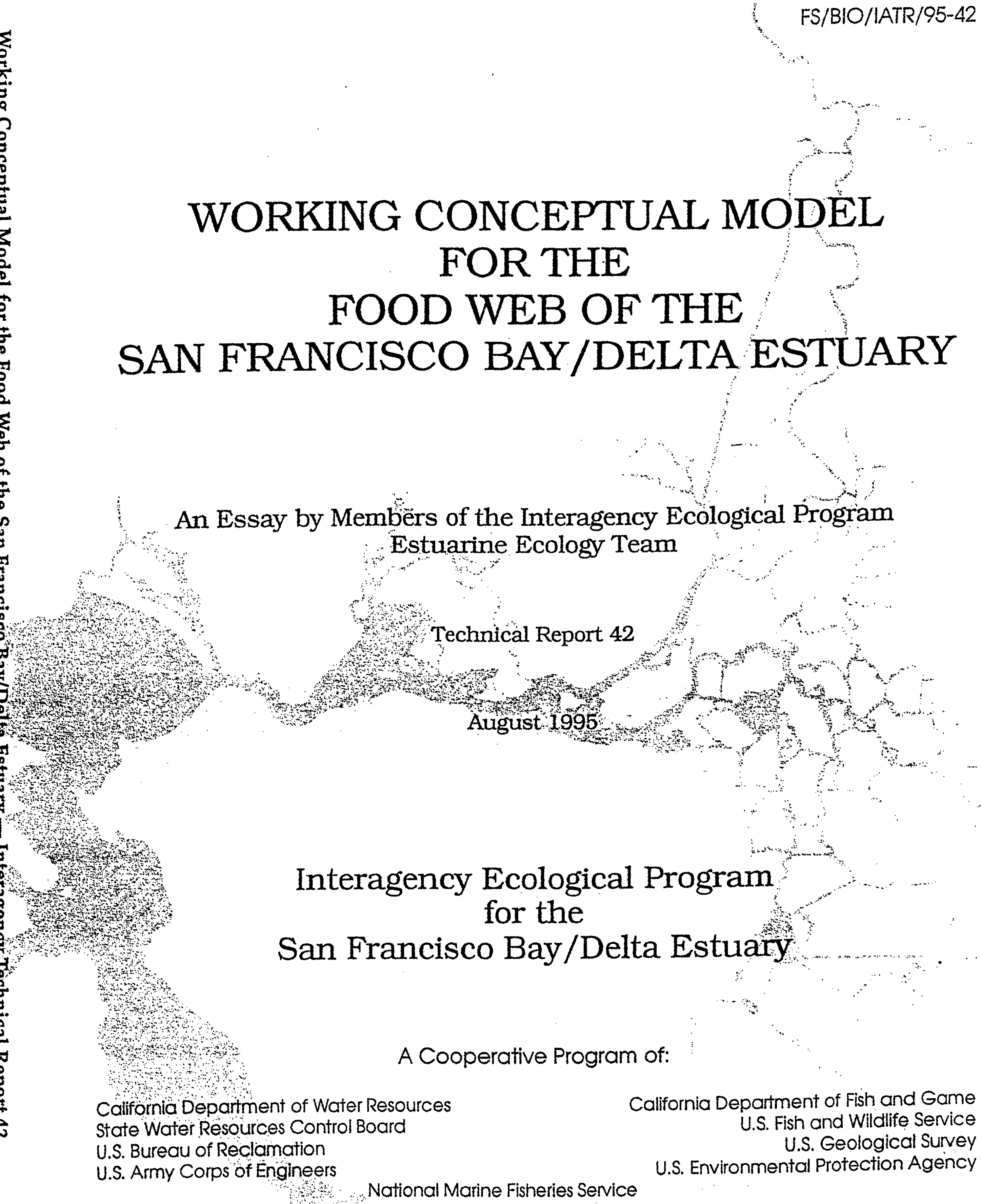

WORKING CONCEPTUAL MODEL FOR THE FOOD WEB OF THE SAN FRANCISCO BAY/DELTA ESTUARY

An Essay by Members of the Interagency Ecological Program
Estuarine Ecology Team

Technical Report 42

August 1995

Interagency Ecological Program for the San Francisco Bay/Delta Estuary

A Cooperative Program of:

California Department of Water Resources
State Water Resources Control Board
U.S. Bureau of Reclamation
U.S. Army Corps of Engineers
California Department of Fish and Game
U.S. Fish and Wildlife Service
U.S. Geological Survey
U.S. Environmental Protection Agency
National Marine Fisheries Service

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SUMMARY

This conceptual model is an attempt to describe our current understanding of the bay-delta ecosystem, with emphasis on the lower trophic levels. This model focuses on what is known about this ecosystem and what needs to be learned. The objectives of the study were to assemble and display the status of knowledge of lower trophic levels in the estuary, examine the gaps in that knowledge, and establish and prioritize a set of research questions. We hope that this can serve as a "living document" that will be updated from time to time as new knowledge becomes available.

Part I of this report describes the current state of understanding of lower trophic levels of the estuary. Part II contains a discussion of information needs, organized around a set of research questions aimed at understanding key aspects of bay-delta ecology.

The extent of knowledge of estuarine ecology varies with discipline. Knowledge of estuarine hydrodynamics is reasonably well advanced, and improving rapidly. We have an increasing grasp of how hydrodynamic conditions affect water quality and the movement of substances and, to a lesser extent, particles and plankton. Monitoring and other studies in the San Francisco Bay-Delta estuary have resulted in a huge data set on abundance patterns and species composition of some functional groups, including phytoplankton, zooplankton, benthic macrofauna, and especially fish. We know the major influences on phytoplankton biomass and production and understand conceptually the retention of organisms in the estuary.

Efforts to monitor the estuary have done little to provide understanding of the causes of observed patterns or the relationships among these groups or between them and external forcing such as freshwater flows and exports. For example, quantitative relationships exist between abundance or survival of many different kinds of organisms and flow conditions in the estuary, but in most cases we do not know why.

Several wide gaps exist in our knowledge of the ecology of the estuary. The largest general areas of ignorance are:

- Mechanisms behind many of the effects of flow on the biota.
- Interaction of behavior and circulation patterns in maintaining populations.
- Factors that influence the success and effects of introduced species.
- Effects of toxicants on populations.
- Biological interactions (predation, competition) in any part of the estuary.
- The role and importance of phytobenthos, microzooplankton, and microbenthos in the ecosystem.

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Figures

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Part I
CURRENT UNDERSTANDING

This document presents a conceptual model of the food web in the San Francisco Bay/ Delta Estuary. The model focuses on what is known about this ecosystem and what needs to be learned. It is constructed as a series of assertions about the important cause/effect relationships in the estuary and a series of questions that can be used to guide future research and monitoring efforts.

This is not a review paper, and we have put little effort into literature review. Instead, we have relied on our own collective understanding based on the several years of analysis and literature review that the Estuarine Ecology Team (formerly Food Chain Group) and others have conducted. Although a comprehensive conceptual model would require extensive literature citations, the time required for this would be excessive. Thus, this is the current "best guess" of the members of this team, not a scientific paper in the traditional sense. Sources we have drawn on are listed below.

The model presented here can be thought of as a snapshot, outdated before it goes to print. Much is being learned by the bay/ delta scientific community, and scientific opinions on some of these topics are changing. Thus, this document should serve as an indication of where we are now, and perhaps in the future as a means of assessing what has been learned. If this exercise proves useful, periodic updates of this document might be used to focus attention on the progress being made by the bay/delta scientific community. Thus, this could become a "living document" that would be brought up-to-date by experts in various disciplines.

Objectives and Scope

The objectives of the study were to assemble and display the current status of knowledge of lower trophic levels in the estuary, examine the gaps in that knowledge, and establish and prioritize a set of research questions.

Most of the emphasis in the model is on lower trophic levels: phytoplankton, zooplankton, and macrobenthos. We have included some discussion of fish but emphasize early life history. We also discuss the abiotic environment, including the direct and indirect effects of freshwater flow and tides.

We have defined the bay to exclude marshes, although there are clearly cause-and-effect relationships that cross this boundary. The marsh is considered only as a source of organic matter or as nursery habitat for fish. Furthermore, none of us has particular expertise in marshes. Similarly, we have not addressed macrophytes or wildlife.

Sources of Information

The information presented here can be found in one form or another in a variety of published and unpublished references. Several of these references are particularly useful in providing summaries of the information available about some aspect of the estuary. These include:

- Several published volumes on aspects of estuarine ecology.
- Status and Trends reports prepared for the San Francisco Estuary Project.
- Agency testimony to the State Water Resources Control Board.

- Interagency Program and agency technical reports.
- Technical reports on the ecology of the entrapment zone.
- A report on effects of flow and flow standards for the San Francisco Estuary Project.
- Papers by Cloern, Jassby, Nichols, and colleagues on ecosystem dynamics in various parts of the estuary.
- Papers by Carlton and colleagues on species introductions.

Organization of the Conceptual Model

This model focuses on cause-and-effect relationships. We have omitted discussion of known interactions that we believe have little influence. Highly subjective choices have been made about the degree of importance of relationships and the degree to which they are understood. No two investigators would make identical choices.

The ecosystem has been divided up for discussion into the upstream region, the entrapment zone, and downstream. Obviously these overlap to some extent, in that the entrapment zone is often in the delta and the boundary between the entrapment zone and the downstream area is poorly defined. The entrapment zone is defined approximately by the salinity range 1-6 parts per thousand (ppt), while the downstream region is the part of the north bay at higher salinities, and the upstream or delta region extends from 1 ppt to about the upstream limit of tidal action. Thus the entrapment zone includes the historical locations of the turbidity maximum and peaks in populations of *Eurytemora* and *Neomysis*; larvae of striped bass and delta smelt, which congregate just upstream of the entrapment zone, are also discussed as entrapment zone species. To highlight factors common to all regions, we first present a conceptual sub-model for the estuary as a whole.

This may be the first-ever attempt to develop a conceptual model without a single flow diagram. Having found such diagrams uninformative in discussing causative links, we opted instead to summarize the model in a series of cause-effect matrices (Figures 1-3), one applying to each area. Causes are listed, and briefly described as necessary, in Table 1. Note that not all causes apply in all areas. The following section describes the matrices in detail.

The conceptual models presented here refer primarily to the dry season, or to dry years. Effects of increased outflow are discussed where appropriate. Wet seasons are characterized by increased flow, reduced proportion of water diverted, and lower temperatures, all of which appear to favor abundance or survival of many estuarine species.

Effects Matrices

The effects matrices (Figure 1-3) are organized with causes down the left column and effects across the top. Symbols represent the magnitude of the effect (large, small), and the degree of understanding of that effect (high, low). For example, in Figure 1 freshwater inflow is asserted to have a large effect on toxicants that is poorly understood. Blanks indicate that there is no effect or that it is likely to be unimportant. Letters are used to represent rows, and numbers columns, for cross-referencing between the text below and particular cells in the matrices.

The importance of each effect is judged by the degree to which that causative relationship influences the affected variable. This is not to assert that the causative relationship is necessarily of great importance to the ecosystem, or to management of the estuary. For example, the assertion in the previous paragraph that freshwater flow is important to toxicant concentrations does not imply that toxicants are necessarily important to the biota.

	EFFECTS / CAUSES	Primary	1 Freshwater Inflow	2 Agricultural Diversions	3 Exports	5 Tidal Forcing	6 Wind Mixing	7 Dredging	8 Discharges	9 Toxicants	10 Species Introduction	11 Temperature	Intermediate	12 Dissolved O_2	13 Salinity (Agricultural)	16 Residence Time	20 Resuspension	21 Nutrients	22 Exogenous Carbon	23 Transparency	Biological Direct	24 Phytoplankton	25 Microzooplankton	26 Zooplankton	27 Benthos	28 Fish	Biological Indirect	Phytoplankton	Microzooplankton	Zooplankton	Benthos	Fish
										Environmental Effects																						
	Primary																															
A	Freshwater Inflow		■							●	●	∘		○	○	●	•	●	●	●		●	●	●	●	●		●	●	●	●	●
B	Agricultural Diversions			■						•						●			•	●		●	●	●	•	●		•	•	•	•	•
C	Exports				■					•		∘			∘	●			•	•		●	●	●	•	●		●	•	•	•	•
E	Tidal Forcing					■				•	•					●	○		•	○		•	•	•	•	•		•	•	•	•	•
F	Wind Mixing						■									•	○			∘		∘			•			•	•	•	•	•
G	Dredging							■		•	∘			○			•	•		∘					○							
H	Discharges								■	○		∘		•	○		•	●	•			•	•					•	•	•		•
I	Toxicants									■												∘	•	●	•	●						•
J	Species Introduction										■											●	●	●	●	●		●	●	●	●	●
K	Temperature											■		○								○	○	○	○	○						
	Intermediate																															
L	Dissolved O_2													■										∘	∘	∘						
M	Salinity (Agricultural)														■							•	•	•	•	∘						
P	Residence Time									•	•	•		○		■		•		∘		○	●	●	•	●						
T	Resuspension									•						•	■	•		○		○	•	•	•	∘						
U	Nutrients																	■				○										
V	Exogenous Carbon													•					■	•		•	•	•	•							
W	Transparency																			■		○	•	•		•						
	Biological																															
X	Phytoplankton													○				○		○		•	●	●	●	•						
Y	Microzooplankton																	○				●	●	●	•	•						
Z	Zooplankton																					●	●	●	●	●						
AA	Benthos																•	∘		●		●	●	•	●	•						
AB	Fish																						•	•	•	●						

Biological Effects

Indirect Effects

LEGEND

- ○ Large effect, relationship well understood
- ∘ Small effect, relationship well understood
- ● Large effect, relationship poorly understood
- • Small effect, relationship poorly understood

Figure 1
EFFECTS MATRIX FOR THE UPSTREAM AREA

	CAUSES \ EFFECTS	Primary	1 Freshwater Inflow	2 Agricultural Diversions	3 Exports	5 Tidal Forcing	6 Wind Mixing	7 Dredging	8 Discharges	9 Toxicants	10 Species Introduction	11 Temperature	Intermediate	14 Stratification	15 Position of Salt Field	16 Residence Time	17 Lateral Circulation	20 Resuspension	21 Nutrients	22 Exogenous Carbon	23 Transparency	Biological Direct	24 Phytoplankton	25 Microzooplankton	26 Zooplankton	27 Benthos	28 Fish	Biological Indirect	Phytoplankton	Microzooplankton	Zooplankton	Benthos	Fish
			Environmental Effects																				Biological Effects						Indirect Effects				
	Primary																																
A	Freshwater Inflow		■						o	•	•	o		○	○	●	●	o	○	●	○		•	•	•	•	•		●	●	●	●	●
B	Agricultural Diversions			■																•	•		•	•	•		•		•	•	•	•	•
C	Exports				■										○	•				•	•		•	•	•		•		•	•	•	•	•
E	Tidal Forcing					■						o		○	○	●	●	○		•	○		•	•	•	•	•		●	●	●	●	●
F	Wind Mixing						■					o		○		•	●	○			○		•	•	•	•			●				•
G	Dredging							■		•	o							•			o					o							•
H	Discharges								■	•		o							o	•							•		•	•	•		•
I	Toxicants									■													•	•	•	•	•						•
J	Species Introduction										■												●	●	●	●	●		●	●	●	●	●
K	Temperature								o			■											○	○	○	○	○						
	Intermediate																																
N	Stratification						o							■	●	●	•	•			○		○	●	•	•	•						
O	Position of Salt Field										•	•		•	■	●	●	•	•	•	•		○	●	•	○	o						
P	Residence Time									•	•					■					○		○	●	●	•	●						
Q	Lateral Circulation											•		•		●	■			•	•		●	●	●	•	●						
T	Resuspension									•						●		■	•		○		○			•							
U	Nutrients																		■				o										
V	Exogenous Carbon																			■				●	•	●							
W	Transparency																				■		○				•						
	Biological																																
X	Phytoplankton																		○		o			●	●	●							
Y	Microzooplankton																		○				•	●	●	●	•						
Z	Zooplankton																						o	●	●	●	●						
AA	Benthos																	•	o		•		○	●	●	●	●						
AB	Fish																							•	●	●	●						

LEGEND

- ○ Large effect, relationship well understood
- o Small effect, relationship well understood
- ● Large effect, relationship poorly understood
- • Small effect, relationship poorly understood

Figure 2
EFFECTS MATRIX FOR THE ENTRAPMENT ZONE AREA

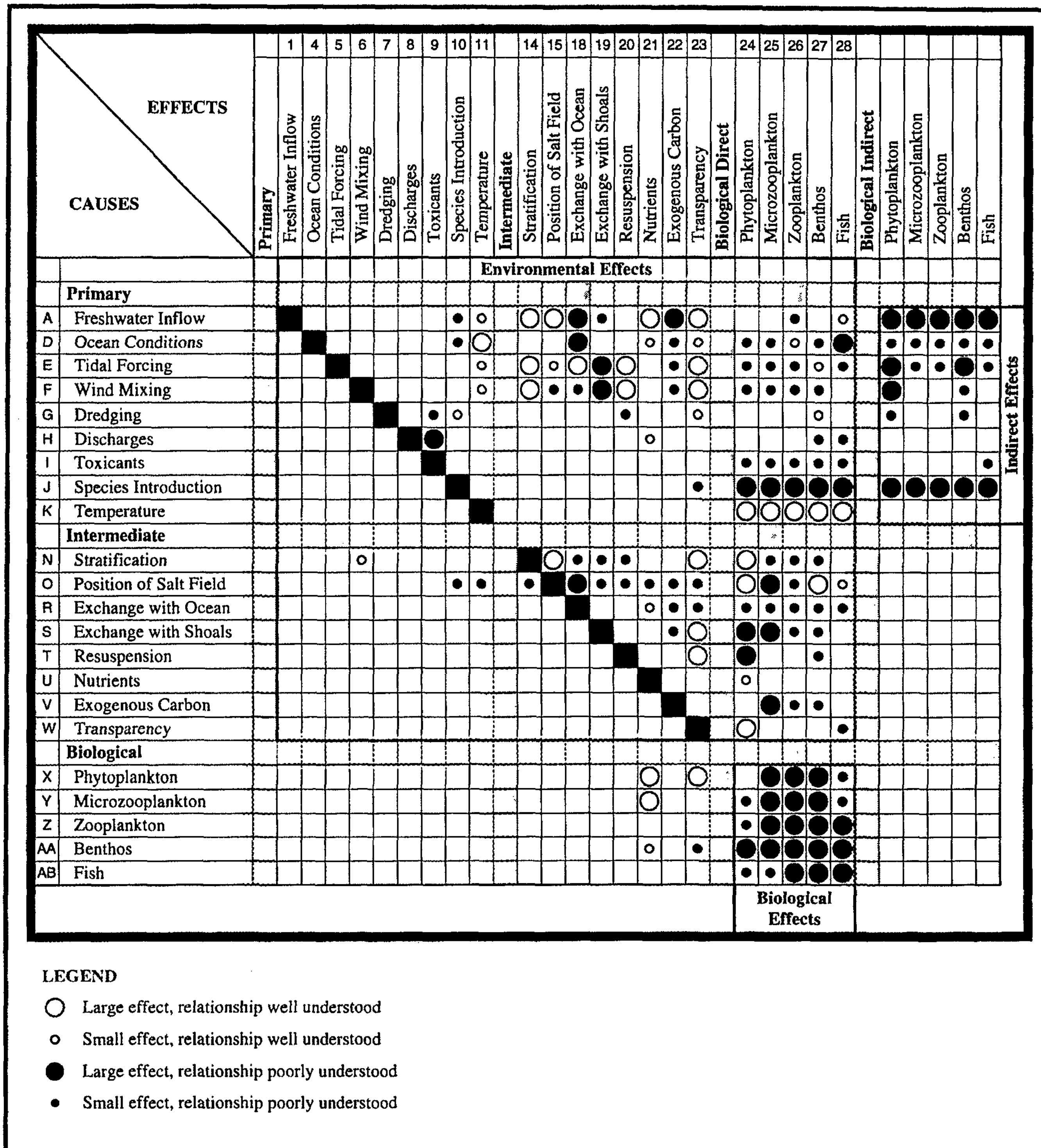

Figure 3
EFFECTS MATRIX FOR THE DOWNSTREAM AREA

Table 1
CAUSES DEPICTED IN THE EFFECTS MATRICES

Each applies to all areas except where noted: U=upstream, E=entrapment zone, D=downstream.
Letters and numbers in left margin refer to positions in matrix diagrams.

	CAUSE	REGION	EXPLANATORY NOTES
Primary Causes			
A1	Freshwater inflow		Inflow to area of interest: approximately delta inflow for upstream, delta outflow for EZ and downstream
B2	Agricultural diversions	U, E	Total withdrawals within the delta other than the major water projects
C3	Export flows	U, E	Water withdrawals by the projects
D4	Ocean conditions	D	Temperature, level, and content of nutrients and biota
E5	Tidal forcing		External forcing by the tide, resulting in most of the dispersion within the estuary
F6	Wind mixing		
G7	Dredging		Direct effects of dredging and disposal
H8	Discharges		Includes sewage, industrial, agricultural, and other inputs
I9	Toxicants		Includes agricultural and industrial chemicals
J10	Species introductions		As a general category; specific introduced species are discussed in biological causes
K11	Temperature		
Intermediate Causes/Responses			
L12	Dissolved oxygen	U	Not a factor except in the San Joaquin River
M13	Salinity (agricultural)	U	Dissolved salts coming from agricultural runoff
N14	Stratification	E, D	
O15	Position of salt field	E, D	Can be indexed with X_2
P16	Residence time	U, E	Refers to residence time of particles, but loosely defined. Discussed under Exchange with Ocean in Downstream area
Q17	Lateral circulation	E	Includes exchange with shoals of Suisun Bay and residual circulation through northern channels.
R18	Exchange with ocean	D	Effectively, the inverse of residence time in the downstream area
S19	Exchange with shoals	D	Similar to lateral circulation above, but only between single channels and adjacent shoals.
T20	Resuspension		Refers to both inert particles and biota
U21	Nutrients		Dissolved inorganic nutrients
V22	Exogenous carbon		Exogenous to the estuary as a whole
W23	Transparency		
Biological Causes/Responses			
X24	Phytoplankton		Biomass, productivity, or abundance
Y25	Microzooplankton		Biomass or abundance
Z26	Zooplankton		Abundance
AA27	Benthos		Abundance
AB28	Fish		Abundance or survival

There are three categories of causes (Table 1). Primary causes are forcing functions, i.e. variables that affect the ecosystem but for the most part are not affected by it. For example, tidal forcing is unaffected by whatever else is happening within the estuary. Some exceptions exist: for example, agricultural diversions and exports can affect the amount and location of freshwater flow entering the upstream area, but they are considered primary causes.

Intermediate causes are physical and chemical variables that depend on various (mainly physical) causes, and that in turn affect each other and the biota. For example, dissolved oxygen is affected by several flow variables, as well as inputs of organic matter from exogenous sources or phytoplankton, and can affect biota.

Biological cause-effect relationships include feeding and predatory interactions, whose importance may or may not be mutual. For example, in the entrapment zone (Figure 2) zooplankton have a small effect on phytoplankton, but phytoplankton can have a large effect on zooplankton.

Indirect effects indicate pathways by which primary causes influence biota through intermediate variables. For example, in the downstream area freshwater flow has little or no effect on the biota directly, but can have considerable influence through its effects on stratification, position of the salt field, exchange, inputs, and transparency.

COMMON FEATURES

1 Here we discuss those aspects of the model that apply to all regions, and the degree to which the various causal relationships are understood. The discussions of individual regions contain only the aspects that are unique to those regions. Paragraph numbers are given for cross-referencing the information gaps in Part II.

2 In this and subsequent sections we begin the discussion with direct environmental effects, including interactions between various aspects of the physical and chemical environment. These effects are depicted in Figures 1-3 as "Environmental effects". The next section discusses how the physical and chemical environment directly affects each group of biota. The next two sections discuss biological effects, shown at the bottoms of the figures, and indirect effects, shown at the right.

Direct Environmental Effects

3 Recent improvements in technology are making possible significant advances in understanding of the physical environment of the estuary. These include models such as particle-tracking models and the 3-dimensional models under development, and measuring devices such as the acoustic doppler current profiler (ADCP) and ultrasonic velocity meter (UVM), which are revolutionizing the measurement of currents. Although equivalent modern techniques are being developed elsewhere for analysis of biological systems, their use in this estuary has not kept pace with these rapid developments in physics.

4 **Freshwater flow** refers to the inflow of water into each region. This means *approximately* net delta inflow for the upstream region, and net delta outflow for the entrapment zone and downstream regions. This is approximate for the upstream and entrapment zone regions because the boundaries of these regions are variable.

5 Freshwater flow has some effects, mostly indirect, throughout the bay. Freshwater outflow determines the tidally-averaged longitudinal position of the salt field, and therefore the geographic boundaries of the 3 regions. The upstream boundary of the entrapment zone, and other habitat characteristics, have been indexed by the longitudinal position of 2 ppt salinity at the bottom, referred to as X_2. (A15)

6 Many variables are correlated with freshwater flow. There is a nearly linear relationship between X_2 or the position of any salinity value and the log of net delta outflow. This implies that the longitudinal density gradient becomes steeper with increasing outflow, possibly resulting in stronger estuarine circulation. Outflow is positively correlated with river flows into the delta, and inversely with the proportion of water exported. These close correlations with outflow obscure the causes of apparent responses of biota to flow.

7 Residence times of water each sub-embayment generally decrease as freshwater flow increases. Freshwater entering the estuary brings nutrients and organic carbon, and can reduce transparency through transport of suspended matter. Inputs of nutrients and particles to the downstream and entrapment zone regions depend on freshwater flow in a fairly predictable way, but in the upstream area these effects are obscured by flow patterns within the delta. (A16, 18, 21, 22, 23)

8 Effects of freshwater inflow on temperature, stratification, dissolved oxygen (upstream), and salinity resulting from agricultural drainage (upstream), are large and reasonably well understood. Effects of freshwater inflow on downstream circulation patterns are less well understood; effects of increasing freshwater flow presumably include increased density-driven residual circulation and reduced residence time. (A11, 14, 12, 13)

9 Effects of flow on species introductions are inferred from the timing and location of major invasive successes. Alterations of habitat conditions that reduce the abundance of extant species may open habitat for invaders, as in the drought of 1987-88. (A10)

10 Direct effects of flow on biota are poorly understood, but are probably large only in the upstream area. High flow can move pelagic organisms downstream. Deliberate releases of large pulse flows may be useful in moving species of concern through the delta. Further downstream, effects of flow are still large but predominantly indirect, through position of the salt field, stratification, and other intermediate variables. (A24-28)

11 **Agricultural diversions** within the delta can alter internal flow patterns, probably also influencing freshwater flow to the entrapment zone and thereby the position of the salt field. Presumably agricultural diversions influence residence time and transparency in the delta, and have major effects on pelagic biota by removing them. No effects on the downstream area are to be expected. (B16, 23-28)

12 **Exports** have similar effects to agricultural diversions, with substantial effects on all pelagic organisms within the upstream area. Exports can also have an effect on the position of the salt field, since export flows determine the large-scale net movement of water through the delta. (C15, 16, 23-28)

13 **Ocean conditions** provide an endpoint for the downstream region; thus oceanic temperature influences the bay, and sea surface elevation can affect exchange between the bay and the ocean. Biological effects arise through the influence of upwelling and El Niño, and through the supply of fish and benthic larvae that are recruited to the bay from the coastal ocean. (D18, 24-28)

14 **Tidal forcing** is the principal cause of dispersion in the estuary, and has major effects in setting up stratification, dispersing substances and biota, eroding shorelines, and resuspending sediments, as well as minor effects on temperature and the longitudinal salinity gradient. Tidal flows are believed to be responsible for most of the longitudinal

transport of salt. This transport is probably accomplished mainly by tidal trapping and tidally-driven residual circulation, both of which are enhanced in areas where major bathymetric features are closer together than the tidal excursion. (E11, 14-20, 22-28)

15 Exchange between shoals and channels, driven largely by tides and wind, is poorly understood. (E17, 19)

16 **Wind mixing** affects circulation primarily over shoals, where shallow downwind currents can develop, which are then balanced by residual counter-currents in channels. Wind mixes the water column over the shoals to the bottom and resuspends sediments. Wind speed can sometimes be high enough to disrupt stratification in channels. Effects on temperature and the salt field are smaller. The effect of wind on exchange between shoals and channels is poorly understood, and likely to be an important mechanism for mobilizing sediments that are then transported off the shoals. Probably the most important biological effect of wind is on resuspension, resulting in reduced light penetration and phytoplankton growth. (F14, 19, 20, 23)

17 **Dredging** The principal effect of dredging is to remove sediment from one area and deposit it in another, with attendant loss to resuspension. The annual volume of dredging is about the same magnitude as the mean input of sediments by the streams. The magnitude of natural resuspension and settlement of sediments in the bays is unknown, so these cannot be compared quantitatively with dredging. Sediment in some areas, particularly near industrial sites, is highly toxic, and dredging releases the toxicants into the water. So far, no population-level effect on any species has been ascribed to dredging, although obvious local effects occur through removal or burial of benthic organisms. (G9, 20)

18 **Discharges** of municipal, industrial, and agricultural wastes release nutrients, salt, pesticides, particulate matter, and organic matter into various parts of the estuary. Releases of organic matter from sewage treatment plants, responsible for severe oxygen depletion in the past, have decreased over the last few decades with improved treatment. However, it is possible that this decrease has led to reduced abundance of some planktonic organisms, with possible effects on fish populations. (H9, 12, 13, 21, 22)

19 **Toxicants** are of concern throughout the estuary. No population-level effects have yet been shown to result from toxic inputs. This is partly because of a number of difficulties with measuring toxic materials, and with determining population-level effects of any change in environment. Evidence suggests that such effects should be expected in some parts of the estuary. (I24-28)

20 **Species introductions** as a general concept is difficult to address, since its effect depends on the particular species. It is included as a separate, primary effect because species introductions in general have had about as much effect as any other anthropogenic change in the estuary in the last 2 decades. (J24-28)

21 The bay/delta is notable for the number of invasions by exotic species. Most of the benthic species of the bay are exotic, as are many of the fish and zooplankton now abundant. Yet, it would be difficult to make generalizations about the susceptibility of the estuary to particular kinds of invaders. The effects of particular introduced species can be instructive in determining the important controls in the ecosystem. However, we cannot make a general statement about the effects that the next introduced species might have. Thus, our discussions of introduced species are largely devoted to the few that have been studied owing to their obvious effects. (J24-28)

22 **Temperature** is the best-understood variable in terms of its determinants and its biological effects. Water temperature is determined mainly by air temperature and mixing of different water masses. Temperature sets rate constants for biochemical reactions and therefore has an overriding

influence on all of the trophic groups and on dissolved oxygen. Seasonal patterns of abundance can generally be considered responses to changes in temperature or light levels. (K12, 24-28)

23 **Dissolved oxygen** can be depressed by excessive biological oxygen demand. Although reduced oxygen is a major problem in many estuaries, it has only localized effects on benthos and fish in the Stockton Ship Channel. (L27, 28)

24 **Agricultural salinity** has poorly known, but probably minor, effects, except that striped bass spawning can be blocked by high salinities in the San Joaquin River. (M24-28)

25 **Stratification** can affect the longitudinal salinity distribution, residence time of particles, and water transparency; these effects are understood at least qualitatively. Stratification has minor but poorly understood effects on exchange between shoals and channels. Stratification may also insulate organisms in the water column from the effects of benthic consumption; this has been noted for phytoplankton blooms in South San Francisco Bay. (N15-20,23-25)

26 **Position of the salt field** has large, poorly understood effects on longitudinal dispersion and therefore residence time (entrapment zone) or exchange with the ocean (downstream). It has similar effects on lateral circulation in the entrapment zone, in that lateral circulation is influenced by the bathymetry surrounding the entrapment zone. Most of the other intermediate causes (e.g. exchange with shoals, resuspension, nutrients, exogenous carbon, transparency) are somewhat influenced by the position of the salt field. (O16-23)

27 Distributions of pelagic biota are more closely linked to the position of the salt field than to geography. Position of the salt field can affect the abundance of populations at a given salinity or over their entire range, through interactions with bathymetry. Phytoplankton biomass is higher when the entrapment zone is adjacent to shoals than when it is in channels, and this effect may carry through to animals. Benthos are affected differently, in that their habitat is defined by mean salinity over a time scale of weeks to months. (O24, 27)

28 **Residence time** of particles is poorly understood as a concept, and would be difficult to measure. Residence time can be defined as the extant concentration of particles in a region, divided by their rate of removal. Thus it implies a relationship with rates of mixing and advection of particles, and the concentration mechanisms that are believed to operate in the entrapment zone. Particles that settle would generally have a longer residence time in an area because they would move more slowly than the mean flow of tidal currents. Presumably residence time has major effects on transparency in the entrapment zone, and on dissolved oxygen in the upstream area. (P12, 23)

29 Residence time of biota is more complicated than that of particles. All pelagic populations living in an estuary must have mechanisms to overcome losses due to dispersion or advection away from the most favorable habitat. These mechanisms can be as simple as a high population growth rate, which serves to offset losses unless the rate of loss is excessive. Larger organisms such as fish have enough control over their position to overcome advection and dispersion except in larval stages. Zooplankton including larval forms of fish and benthic species can adjust vertical position, and phytoplankton are often negatively buoyant and therefore sink in the water column. In a medium of vertically variable tidal flows, these behaviors can maintain these populations within a relatively narrow range of salinity, and offset the effects of dispersive losses. This effect of vertical positioning has been inferred from observations of vertical migration and assumptions about flow rates, but actual rates of horizontal movement and retention have not yet been determined. (P24-28)

30 **Lateral circulation** refers to exchange between the main channel and shoals as well as other channels. Lateral circulation presumably affects residence time of particles in the entrapment zone, and movement of organic and inorganic particles. In addition, there is good evidence that phytoplankton are affected by lateral circulation, and we assume but cannot show that other pelagic organisms are similarly affected. (Q16, 22-28)

31 **Exchange with ocean** is an alternative term embodying the concept of residence time (downstream). Variations in exchange have relatively minor effects, mainly in terms of import of larvae and mixing of pelagic biota and materials in and out of the bay. (R21-28)

32 **Exchange with shoals** affects transparency through the movement of resuspended particles. This presumably has an effect on phytoplankton and also on microzooplankton, but probably less on other biota. (S22-27)

33 **Resuspension** reduces transparency, and lifts from the bottom phytoplankton cells that have settled. Resuspension interacts with tidal transport to affect residence time of particles in the entrapment zone. It could have a minor effect on benthos, although erosion of sediments in some areas (e.g. Carquinez Strait) alters the substrate and almost certainly limits the range of biota that can settle there. (T16, 23-24, 27)

34 **Nutrient** effects on phytoplankton and perhaps phytobenthos and microzooplankton are limited to bloom periods when nutrients can become exhausted; this seems to be a major effect only briefly in the upstream region. (U24, 25)

35 **Exogenous carbon** is poorly known. Calculations have shown the probable importance of exogenous carbon in the northern reach of the estuary. High bacterial production relative to primary production in the entrapment zone and downstream implies an external source of carbon, which would be available to microzooplankton and benthos, and indirectly to other biota. (V25-27)

36 **Transparency** controls production of phytoplankton and benthic plants, and is therefore a key control on food-web dynamics, in much of the estuary. Turbidity may interfere with visual predation. (W24, 28)

Biological Responses to Environment

37 Direct environmental effects arise primarily from the intermediate effects discussed above. For example, direct effects of freshwater flow on most biota of the estuary are unlikely, but flow can affect the biota through stratification, salinity distribution, and residence time. Direct effects of tide and wind on pelagic populations are unlikely to be very important except in local areas of high shear or turbulence. However, direct effects on the benthos through scouring and resuspension of biota are likely to be important at least locally. (A, E, F24-28)

38 Species introductions in general have a major but poorly defined effect on the biota, although in certain cases the effects are better understood. The effect of temperature is well understood in general for all biota. Similarly, the effect of the salt field is to regulate the longitudinal distribution of all estuarine biota, although the time scale for regulation of benthic organisms is much longer than that for pelagic organisms. (J, K, O24-28)

39 **Phytoplankton** As in other oceanic and estuarine study areas, the phytoplankton are known primarily through measures of biomass and production rather than species composition. Counts of some species have been made in samples from the upstream and entrapment zone regions, but questions exist about the historical reliability of identifications and abundance estimates.

40 Phytoplankton growth rate throughout the estuary is controlled mainly by light, with nutrient concentrations having little or no effect except when they are depleted during blooms. The Cole-Cloern model, by which primary production can be estimated from

chlorophyll, incident radiation, and transparency, works well throughout the estuary. Biomass appears to be determined by growth rate, physical exchange, and benthic grazing. Because of high turbidity in much of the bay, phytoplankton production in San Francisco Bay is lower than in other estuaries of similar dimensions. (W24)

41 The effect of exchange with shoals on phytoplankton biomass and production is poorly understood. In Suisun Bay, exchange between shoals and channels is instrumental in enhancing biomass in the entrapment zone because of high light penetration to the bottom over the shoals. In San Pablo Bay in summer, turbidity is greater in the shoals than in the channels, possibly counteracting the effect of shallow water on light available to phytoplankton. (Q, S24)

42 **Microzooplankton** Virtually nothing is known of the microzooplankton of the estuary except for monitoring data on the abundance of rotifers and copepod nauplii, and data collected in 1993-4 on grazing rates and abundance of protists. Based on information from elsewhere, we would expect to find a vigorous assemblage of microzooplankton including heterotrophic flagellates, ciliates, and other protists. Their dependencies on the abiotic environment should be related to those for zooplankton and phytoplankton. These organisms form part of the "microbial loop", the basis of which is production by phytoplankton and bacteria. (Y)

43 The importance of bacteria in repackaging organic matter has been demonstrated for both Suisun Bay and South Bay. Note that the bacteria are not truly a source of organic matter, but they do make otherwise unusable organic matter available to higher trophic levels. (V,Y)

44 Microzooplankton should be trophically very important. If 5 times as much carbon goes through the bacteria as through the phytoplankton in Suisun Bay, considerable energy could become available to the mesozooplankton through the microbial loop. Thus our predilection to view the phytoplankton as the base of the food chain may have led us to ignore other energy sources, at least in some parts of the estuary. Experimental methods for measuring grazing by microzooplankton in a highly turbid environment are being developed. (V25,26)

45 **Zooplankton** distributions within the estuary are related to salinity, so our division of the estuary into habitats also divides the zooplankton fauna. In general, zooplankton can be affected by physical factors such as advection or mixing out of favorable regions, turbulence, or stratification, but more often populations are limited by biological effects. (O26)

46 Zooplankton abundance in this estuary seems low compared to other estuaries, particularly in view of the high phytoplankton biomass that existed in Suisun Bay before the spread of *Potamocorbula*. Amphipods, abundant since about 1988, have not been identified or examined quantitatively.

47 **Benthos** Throughout the estuary, the benthos consists of various representatives of the mollusks, polychaetes, and crustaceans, many of them introduced. In general, the distribution of benthic organisms is under the control of physical factors: depth, sediment size distribution and organic matter content, the salinity range, and current velocity.

48 Sediment characteristics are affected by current velocities (mainly tidal, plus freshwater flow upstream and wind-driven flow on the shoals) through control on deposition and resuspension, and also by the effects of dredging and dredge spoil disposal. The extent of these effects is unknown; the volume of dredged material is large, but the area directly affected is small relative to the total area of the estuary. (E-G27)

49 Although information is available on the gross characteristics of sediment that affect macrobenthos, there is very little on the chemistry of sediments for much of the bay. We have no idea of the importance of sediments and their fauna and flora in producing, modifying, or oxidizing organic

matter, or in nutrient transformations. Furthermore, very little is known about meiofauna (metazoans smaller than 0.5 mm such as nematodes and harpacticoid copepods), microfauna (mainly protozoans), benthic microalgae, or bacteria, which are responsible for most chemical transformations in the sediments. (AA)

50 **Fish** Since fish range freely throughout the estuary, it is somewhat more difficult to assign them to regions except for portions of their life cycle. In the following sections we will discuss fish that spend significant parts of their lives in each area. For example, freshwater and anadromous fish are discussed in the section on the upstream area. Bay resident fish including marine species are handled in the downstream region, and discussion of fish in the entrapment zone is limited to analysis of a few species that remain in or near the entrapment zone during early development.

51 Several species of estuarine fish and macroinvertebrates increase in abundance when flows increase or, alternatively, when X_2 is in Suisun Bay. Reasons for this vary and in general are not known. It is likely that the reasons for this pattern differ for different species, but that for most the direct cause of the observed relationship is not outflow but one of its correlates (e.g. protection from entrainment, habitat size, dispersal). (A28)

52 Much of the existing information on fish has been obtained from the monitoring programs for fish of commercial or recreational importance such as salmon and striped bass. Much of this effort may not contribute much to understanding the ecology and flow relationships of other species. That is now being rectified as species are added to special status lists, and monitoring programs are being redesigned to target these species.

Biological Interactions (X24-AB28)

53 Most of the biological effects are inferred from knowledge of the biology of the major species. Relatively few biological effects are actually known from field studies of this estuary. Studies to identify significant cause-effect patterns in estuaries are difficult. For example, a trophic relationship between two species is a necessary but insufficient condition to establish a causative relationship, which also requires that one species have an effect on the population dynamics of the other. This could occur through food limitation (prey affects predator) or through significant predatory impact on prey.

54 To the extent that phytoplankton are biologically controlled, it is probably by benthic grazing; zooplankton grazing is probably of minor importance, although the effect of microzooplankton is not well known.

55 In general, studies of predation are made from the perspective of the predator: i.e. what does the species of interest eat? Rarely is predation examined from the perspective of prey to determine the major predators and their impacts. Thus, in this estuary as elsewhere, we have little information on the effects of predation on prey populations.

56 Introduction of the clam *Potamocorbula amurensis* provided an opportunity to observe a number of biological interactions. Dense concentrations of the clam in Suisun Bay have been correlated with reduced phytoplankton chlorophyll concentrations in the overlying water column. Abundances of *Neomysis mercedis* and the copepods *Acartia* spp., *Eurytemora affinis*, and *Sinocalanus doerrii* all declined precipitously in 1987. The declines in zooplankton probably occurred through a combination of food limitation and, for the copepods, predation on the nauplii. In addition, other benthic species are reduced in areas where *P. amurensis* is abundant, probably through consumption of their larvae.

Indirect Effects

57 Indirect effects are shown separately in Figures 1-3 to distinguish them from direct effects. For example, freshwater flow rate probably has few major direct effects on biota except in the upstream area. Indirect effects of freshwater flow are easily demonstrable in the positive responses of several entrapment zone and downstream species to outflow. Indirect effects of flow could arise through any of its correlates including position of the salt field and therefore of habitat for certain species, change in shape and size of the habitat, exposure to export pumping, dilution or introduction of toxic materials, stratification or gravitational circulation, rates of input of particulate or organic matter or nutrients, or water residence time.

58 Tide and wind have important indirect effects on phytoplankton through their influences on stratification and horizontal and vertical dispersion, and on resuspension of sediments and thereby transparency. This is reasonably well understood for the south bay, but the mechanism in the northern reach may differ. The indirect effect of tides on the benthos is assumed to occur through effects on the food supply and on resuspended material.

59 Indirect effects of species introductions are poorly understood. These may come about through, for example, reductions in phytoplankton biomass that are felt through the food chain.

UPSTREAM

60 The upstream region of the San Francisco Bay/Delta is defined to include tidal waters upstream of the entrapment zone. Under extreme flow conditions the seaward limit of the upstream region can range from Rio Vista to central San Francisco Bay; however, under most flow conditions this region includes most of the delta and the tidal portions of the rivers.

61 This region provides habitat to a large variety of freshwater species. In addition, it is a conduit through which anadromous species move to the estuary, and through which nutrients and organic matter are supplied.

62 The most important factor influencing the upstream region is freshwater flow, which is managed to store water in winter and spring months and release it during summer when demand is high and precipitation negligible. Populations in this region may be controlled more by physical variability than by biological interactions, although there is little information on the latter.

63 Freshwater flow interacts with tidal flow in much of the delta to produce a complex circulation pattern. Instantaneous velocities in most of the delta are dominated by tidal effects. These tidal flows are not merely oscillations, but can transport materials longitudinally through tidal trapping and pumping. A realistic view of the movement of substances through the delta must consider both the mass balance of fresh water, which results in net flow from the rivers toward the export pumps and the entrapment zone, and tidal effects, which may be more effective than net flows in moving particles.

Direct Environmental Effects

64 **Freshwater flow** is the most important factor influencing physical and chemical conditions in the upstream region. High freshwater flow increases the volume of the upstream region both by extending its seaward limit and by increasing shallow-water area through inundation. Freshwater flow influences residence time in the delta,

particularly in those regions little affected by tide. (A16)

65 Erosion and resuspension of bottom sediments by high freshwater flow in river channels release sediment into the water, reducing water transparency. Freshwater flow carries nutrients and organic matter into the upstream region; concentrations decrease with increasing flow but loading rate increases. Nitrate, ammonium, orthophosphate, and organic matter also enter the system from point and non-point sources. Freshwater flow also influences the distribution of salt in the region, both by retarding the upstream penetration of sea salt, and by diluting saline return flows from agriculture. High freshwater flows also dilute agricultural pesticides and herbicides released in agricultural return flows, although high runoff flows can increase the rate of discharge of agricultural chemicals. (A9, 13, 21-23)

66 Although water temperature varies mainly with air temperature, increased residence time associated with low freshwater flow can cause water temperature to increase. Low freshwater flows in conjunction with increased water temperature or high biological oxygen demand can also lead to decreased dissolved oxygen concentrations. (A11, 12)

67 This is the only region for which direct effects of freshwater flow on biota are likely to be considerable; however, even here these effects are modulated by tides. Flushing of materials and organisms out of the upstream area is enhanced at high flows, although some zooplankton (e.g. *Sinocalanus doerrii*) are able to maintain position just above the entrapment zone. (A24-28)

68 Freshwater flow not only removes organisms from the Delta, it may provide seed organisms for delta populations of freshwater bacteria, phytoplankton, zooplankton, and larval stages of benthic organisms; however, little is known of the importance of this presumed subsidy to the maintenance of these populations. (A24-28)

69 **Agricultural diversions** remove water and its contents from the upstream region. Net consumption by the ca. 1800 intakes in the delta is estimated in the DAYFLOW data set to be similar in magnitude to export flows and net outflows during most summers. Gross consumption by these intakes is unknown but likely to be much higher. This is the term of concern for removal of plankton, young fish, and organic particles, since most of these would not be expected to survive the use of the water in irrigation. Studies are underway to evaluate the effect of these diversions on fish in the delta. (B16, 24-28)

70 **Export flows** cause considerable losses of young fish through entrainment and through enhanced predation near export facilities. These losses are believed to have significant effects on populations of young striped bass, salmon (particularly the San Joaquin race), and possibly other species. In addition, calculations of chlorophyll balance in the delta show that losses to export pumping are significant. Losses of zooplankton may not be significant to population maintenance. (C28)

71 **Tidal forcing** mixes substances and organisms within the upstream region. In contrast to the static conceptual model of the delta as a region influenced by calculated net flows such as QWEST, this is a highly dynamic region in which tidal dispersion may be more effective in moving substances and planktonic organisms than net flows. Recent results of particle tracking models show that particles released in different parts of the delta have different probabilities of being entrained in the export pumps, depending on the export flow rate and inflow patterns, but also depending heavily on the tidal pattern. Thus, for example, particles (and by inference, organisms) in the lower San Joaquin River may be moved upstream by dispersion more than by net flow. (E16)

72 **Discharges** from several sewage treatment plants release nutrients and organic matter into the upstream area. Although improved treatment has reduced this effect, biological oxygen demand from discharges and in situ

production is frequently sufficient to reduce dissolved oxygen concentrations in the San Joaquin River near Stockton. (H12, 21, 22)

73 **Discharges** may locally affect the amount of phytoplankton and zooplankton in the water column. Phytoplankton and zooplankton often grow in offstream sewage treatment or farm ponds and may be released with the discharge. Releases of salt from irrigated farms discharging to the San Joaquin River can affect delta salinity enough to impede spawning of striped bass. (H24-26, 28)

74 **Toxicants** include agricultural pesticides released at Colusa Basin Drain, where the water can cause 100% mortality to *Neomysis* and larval striped bass in bioassays. In addition, larval bass in the upstream area frequently have liver conditions indicative of toxicity. Changes in farming practices in 1990 have increased photo-oxidation of pesticides used on rice farms, decreasing the concentration in discharges. This decrease corresponded to a decrease in frequency of liver damage in larval striped bass. Diazenon toxicity may also be a problem during late winter when runoff from orchards enters the San Joaquin River. Although there is enough evidence to suggest that toxicity is harmful to individual organisms in the upstream area, in no case has a population effect been demonstrated. (I24-28)

75 Toxicant concentrations are diluted by freshwater flow. In addition, toxic effects may be modulated by adsorption onto particles advected in by the rivers. (A9)

Biological Responses to Environment

76 **Phytoplankton** include freshwater and estuarine diatoms such as *Thalassiosira* spp., *Cyclotella* spp., *Skeletonema* spp. and *Melosira granulata*, in addition to some green and flagellate species. *M. granulata* is of particular interest in that it forms extensive blooms of long chains of cells that clog sampling nets and may interfere with feeding of some organisms or provide a prey refuge for others.

77 The principal direct environmental effects on phytoplankton appear to be from freshwater flow, residence time, and water transparency. Freshwater flow provides a subsidy of freshwater phytoplankton to the upstream area; in other estuaries, similar subsidies provide the major source of organic matter to the freshwater and brackish regions, but this source may not be as important here. The delta acts as a net producer of phytoplankton, which are removed by export flows, delta outflow, or pumping within the delta. The interaction of inflow, export flow, residence time, and presumably benthic grazing determines the extent to which biomass can build up in the delta, and the degree to which this biomass is exported to the entrapment zone. (A, P, W24)

78 Water transparency is a major factor determining phytoplankton growth, since light is limiting in most of the estuary. The effect of the continued increase in water transparency in much of the estuary over the last 10 to 20 years is unknown, but production per unit biomass has almost certainly increased. (W24)

79 Nutrients are usually in excess except during large phytoplankton blooms. These blooms deplete the water column of nitrate and ammonia but rarely deplete concentrations of silica and orthophosphate. Thus, nutrient concentrations are a poor predictor of phytoplankton production in the upstream area. (U24)

80 Large phytoplankton blooms can alter water quality conditions by depleting nutrients, reducing transparency, and increasing biological oxygen demand. (X12, 21)

81 **Zooplankton** resident in the upstream region include freshwater cladocerans, copepods, and rotifers, and a few species of rotifers and copepods (*Sinocalanus doerrii*) that maintain a position just upstream of the entrapment zone. Many of these zooplankton declined in abundance in the 1970s,

possibly because of a reduction in supply rate of organic matter when sewage treatment was upgraded. However, the exact causes of these declines cannot be determined with much confidence.

82 As with phytoplankton, long residence time, particularly in dead-end sloughs and channels, may promote the development of high abundance of some zooplankton. It also seems likely that river flows provide a subsidy of zooplankton to the upstream area. In neither case is there solid evidence to support these ideas. (A, P26)

83 Although plankton of the upstream region is most vulnerable to entrainment by export pumps, there is no correlation between percent of inflow exported and the abundance of *Sinocalanus*, suggesting that the effect of exports is insignificant at the population level. (C26)

84 **Benthos** biomass in the delta is dominated in many areas by the introduced clam *Corbicula fluminea* and the amphipod *Corophium*. Consumption of phytoplankton biomass by the benthos appears to be high; it may limit food availability for other filter feeders, and may also influence water transparency.

85 Epibenthic organisms may also be important in the delta, including the introduced amphipod *Gammarus daiberi*, which has become important in the diets of young striped bass, and crayfish, for which a fishery existed in the past. Crayfish appear to be abundant but declining, and their ecological role is poorly understood. At present there is no sampling program for epibenthic organisms anywhere in the estuary, so the importance of this group overall is unknown.

86 **Fish** occur throughout the upstream area. Anadromous fish use the upstream regions of the delta for spawning, transport of eggs, larvae, and juveniles, and as nursery habitat. These fish include striped bass, 5 runs of salmon, steelhead, American shad, white and green sturgeon, delta smelt, longfin smelt, Pacific lamprey, and river lamprey.

87 Resident fish in the delta include deliberately introduced species such as white and channel catfish, brown and black bullhead, carp, threadfin shad, and centrarchids including redear sunfish, bluegill, crappie, and largemouth bass. Accidental introductions include inland silversides and chameleon goby. Native species include Sacramento splittail and other cyprinids (minnows), prickly sculpin, and tule perch.

88 Flow patterns within the delta have clear effects on at least the anadromous fish. Survival of salmon smolts depends on flow patterns, and is lower when salmon must pass through the interior delta rather than the mainstem Sacramento River. The striped bass young-of-the-year index is negatively related to percent export flow, probably because of entrainment losses of young bass. This contrasts with a lack of apparent effect of exports on zooplankton, perhaps because their continuous reproduction enables them to overcome this loss. The striped bass YOY index is also positively related to outflow, probably because of its inverse relation with exports, dilution of toxicants, or movement of low-salinity rearing habitat away from pumps by high flows. (A, C28)

89 Other mechanisms by which flow may affect fish in the delta are: inundation of shallows to produce habitat for spawning or rearing (e.g. for splittail); dependence of the extent of delta freshwater habitat on flow; and flows that attract adults or stimulate migration of juveniles of anadromous species. (A28)

90 Little is known of the effects of flows and diversions on resident populations. The increase in transparency of the area since the early 1970s may have affected feeding rates of some species, but this is unknown. (W28)

Biological Interactions (X-AB24-28)

91 For the amount of effort that has gone into this region, there is surprisingly little direct, quantitative information on biological interactions. Most of the information that is available is on diets of fish and some zooplankton, as inferred from gut contents. Young stages of striped bass and delta smelt, and presumably other species, consume mostly zooplankton including copepods, cladocerans, and rotifers and epibenthic organisms such as mysids and amphipods. Older, larger fish generally consume more benthic organisms.

92 Some zooplankton in the upstream area consume diatoms and other phytoplankton. *Melosira* can be consumed, but not at high rates or during blooms.

93 The importance of food limitation, competition, or predation to population dynamics is not known for any species in the upstream area (see entrapment zone section for discussion of striped bass and *Eurytemora*).

ENTRAPMENT ZONE

94 The entrapment zone is operationally defined here as the region bounded (instantaneously or averaged over the tidal cycle) by the salinity range of 1-6 ppt. Functionally, it is the region of a persistent estuarine turbidity maximum (ETM) and maxima in abundance of *Eurytemora affinis*, *Neomysis mercedis*, and larvae of fish such as striped bass and delta smelt (which actually occur slightly upstream of the entrapment zone). It is also close to the upstream limit of salt penetration, stratification, and ebb/flood asymmetry in vertical velocity profiles (i.e. 2-directional tidally averaged flow), and encompasses X_2.

95 The term "entrapment zone" is used locally but not commonly in other estuaries. More common terms include ETM (although ETM phenomena can be independent of the entrapment zone), low-salinity zone, and mixing zone. "Entrapment zone" is used here for historical reasons, but the term implies a mechanism that may not work as originally proposed.

96 The entrapment zone oscillates longitudinally on a tidal cycle and its tidally-averaged location oscillates slightly on the spring/neap cycle. The entrapment zone moves rapidly seaward on an increase in outflow due to an increase in tidally-averaged pressure gradient. It moves (perhaps) somewhat more slowly landward on a decrease in flow in response to tide- and density-induced mixing. Most of the longitudinal movement of salt water and fresh water into and out of the entrapment zone is caused by tidal mixing.

97 The relationship of the entrapment zone to benthos is not as clear as for planktonic organisms: although there are some benthic species tolerant of the salinity range in the entrapment zone, they cannot be considered as "entrapment zone species" as can some of the plankton. They reside in an area over which the entrapment zone passes, and are subjected to the same mean salinity as the pelagic organisms, but with a wider variation. Abundance and diversity of the benthos is generally lower in the entrapment zone than either upstream or downstream.

Direct Environmental Effects

98 The fundamental conceptual model of the entrapment zone is well known, but is now undergoing revision. Density-driven gravitational circulation in this region appears to be much less important for particle trapping than previously believed. Tidal currents and tidally-forced turbulent mixing dominate flow conditions in the entrapment zone, and instantaneous gravitational flow may not occur except for brief periods of slack water or dur-

ing periods of high freshwater flow. Asymmetry in vertical velocity profiles between ebb and flood could still account for some trapping of organisms and perhaps large particles. Lateral flows could be very important in trapping particles and organisms, but this has not been determined. (A, E16)

99 **Freshwater Flow** introduces buoyancy to the upstream end of the estuary, and raises the mean water level. The increased level causes net seaward flow, and the buoyancy introduces stratification. Breakdown of that stratification by tidally-generated turbulence results in entrainment of sea water into the freshwater surface layer. The result is a longitudinal salinity and density gradient, which in the absence of tides would produce an upstream flow of salty water at depth. Tidal flows cause upstream dispersion of salt and override these small net pressure- and density-driven flows. The combination of strong tidal flows and weak gradients produces a small ebb-flood asymmetry in which surface flows on average are slightly ebb-dominated and bottom waters flood-dominated. (A, E14, 15)

100 Increasing freshwater flow increases the longitudinal mean sea surface slope, resulting in a larger pressure gradient and a seaward movement of the entrapment zone. This shortens the distance over which the density gradient extends (i.e. from the entrapment zone to approximately the Golden Gate), increasing the gradient. This suggests that residual gravitational circulation becomes stronger relative to tidal dispersion, although there is no direct evidence for this. Theoretical arguments and recent field data suggest that water depth plays a key role in the development of gravitational circulation, such that it is most frequent in deep water. (A15, 16)

101 Residence time for water decreases as flow increases, while residence time for settling particles would increase if the gravitational circulation becomes stronger. The increase in peak turbidity in the ETM with increasing flow supports this hypothesis. (A16)

102 Freshwater flow also brings exogenous materials to the entrapment zone, both nutrients and particles. The exogenous carbon entering the entrapment zone in freshwater flow is believed to be an important subsidy to local production, and this increases with increasing flow. (A22)

103 **Tidal forcing** produces vertical mixing that resuspends particles and tends to eliminate stratification, and longitudinal dispersion that moves salt and particles. Tidal flows also override and mask the longitudinal net or residual flows. In addition, tidal flows produce residual circulation that can mix and transport particles, and nonlinearities in tidal wave propagation can transport particles upstream through Stokes drift. Finally, tidal flows can produce turbidity maxima at wide or deep reaches of the channels, where tidal velocities are reduced. (E14, 20, 23)

104 **Stratification** directly affects vertical mixing and therefore particle transport in the entrapment zone. Stratification is typically present only during neap tide, when it sets up on the ebb and breaks down on the flood. At a bottom salinity of 2 ppt (near the upstream edge of the entrapment zone), stratification is not much affected by freshwater flow except during extreme floods, but downstream of this region stratification can be affected by flow. (N16, 23)

105 Stratification could insulate organisms residing deep in the water column from export, helping them to maintain position. It can also insulate near-surface phytoplankton and possibly zooplankton from benthic grazers. (N24-28)

106 **Lateral circulation** between the shoals, sloughs, and marsh areas adjacent to the entrapment zone could represent a significant source of particles, organic matter, and plankton for the entrapment zone. The importance of lateral circulation to the entrapment zone would depend on the entrapment zone's position relative to shoal and marsh areas, and on the hydrodynamics of lateral circulation, which is poorly understood. (Q22-26)

Biological Responses to Environment

107 The velocity or volume of freshwater flow does not directly affect entrapment zone biota, but the effect of freshwater flow on entrapment zone position, stratification, and lateral exchange presumably affect the zone's biological community indirectly.

108 **Phytoplankton** populations in relation to entrapment zone conditions have received more study than perhaps any other aspect of the estuarine food web. Phytoplankton biomass was generally elevated in the entrapment zone prior to the spread of *Potamocorbula amurensis*. Previous analyses supported the theory that elevated biomass is due to physical trapping, since light penetration is less in the entrapment zone than elsewhere so that growth rate and even productivity is less in the entrapment zone than elsewhere. The elevation of biomass that occurred when the entrapment zone was in Suisun Bay was probably due to a combination of high growth rates over the shoals, exchange between the shoals and the channels, trapping in channels, and downstream movement and entrapment of freshwater phytoplankton. Since 1987, this elevation has not been observed. (A, P, Q24)

109 **Zooplankton** The zooplankton fauna of the entrapment zone comprise several species of copepods and meroplankton. At least two zooplankton species appear to be entrapment zone species: the copepod *Eurytemora affinis*, and the mysid *Neomysis mercedis*. Peaks in the abundance of the introduced copepod *Pseudodiaptomus forbesi* are also found in the entrapment zone. Both *Eurytemora* and *Neomysis* are known to be important food for larval striped bass, delta smelt, and longfin smelt.

110 There is no direct evidence that the environmental conditions of the entrapment zone affect either zooplankton growth or reproductive rates. The abundance of zooplankton in the entrapment zone may result from a concentrating mechanism similar in principle to that for particles, but dependent on behavior. Maintenance of a mean depth below the midpoint of the water column would result in maintenance of longitudinal position if the ebb/flood asymmetry in vertical velocity profiles is large. Alternatively, vertical migration in synchrony with the tide could result in position maintenance. Both mechanisms have been observed in estuarine zooplankton, and there is evidence that they operate in the entrapment zone of the bay/delta. (P26)

111 Position of the entrapment zone has no significant effect on the peak abundance of *Eurytemora*. *Neomysis* abundances are lower when the entrapment zone is upstream. This is apparently not due to entrainment by export pumps, but the reasons for it are unknown. (C, P26)

112 Lateral circulation may affect abundance of entrapment zone zooplankton, but there are no data to support this. Abundances of *Eurytemora* and *Neomysis* were lower in shallower areas of Suisun Bay than in channels. (Q26)

113 **Benthos** The effect of movement of the entrapment zone on the benthos is reasonably well known and is largely a function of salinity tolerance. The time scale for effects is on the order of months to a year. When the entrapment zone moves upstream during a drought, marine species invade Suisun Bay over about an 18-month period (although *P. amurensis* invaded faster than that). When the entrapment zone moves downstream, some marine species are eliminated and, eventually, the range of freshwater species is extended. Thus, an intermediate entrapment zone position in upper Suisun Bay results in the lowest abundance and diversity of mollusks and presumably other benthos.

114 The salinity of interstitial water in the sediments underlying the entrapment zone responds slowly to changes in the overlying water column, providing a short-term buffer to tidal changes in the entrapment zone's water quality. In addition, benthic species have behavioral and physiological adaptations that permit some adjustment to fluctuating salinity. Finally, adult forms are

generally less sensitive to salinity changes than larvae or new recruits. Thus, some species are able to maintain themselves through periods of unfavorable salinity. *Potamocorbula* is apparently able to remain as far upstream as the western delta through periods of high freshwater flow. (O27)

115 The majority of benthic biomass is in filter-feeding species. Particle concentration by the entrapment zone may enhance the food environment of the benthos through an increase in density, supply, and residence time of particulate (including exogenous and locally produced) organic carbon. However, the degree to which the benthos is limited by the supply of food is unknown. (V27)

116 Recruitment may limit the abundance of benthos. Most benthic organisms in the entrapment zone and elsewhere have planktonic larvae. Larvae of all major taxonomic groups of benthos have been shown elsewhere to be capable of using estuarine flow conditions to move to suitable habitat. When floods deplete the salt-tolerant benthic fauna, recolonization requires that larvae move upstream in the estuary, presumably using tidal or residual circulation to do so. (P27)

117 **Fish** The striped bass, *Morone saxatilis*, is not considered an entrapment zone species, since most life stages are found throughout the estuary. However, the greatest abundance of striped bass larval and early juvenile development stages are found in and near the entrapment zone. This abundance pattern suggests that the early stages of striped bass gain some advantage from entrapment zone conditions. The advantages could include food supply, hydrodynamics for positioning, or a refuge from predation in the high turbidity of the ETM. The behavior of bass larvae, by which they are concentrated in the bottom half of the water column, is suited to retaining them in the entrapment zone once they arrive there from upstream. This can be contrasted with longfin smelt, which remain in the upper part of the water column and are dispersed throughout the estuary during high flows. (P28)

118 The threatened delta smelt can be considered an entrapment zone species, since it is concentrated in the entrapment zone during larval development. The abundance of delta smelt may be associated with position of the entrapment zone. The abundance of smelt increased considerably following high outflow in 1993, supporting the contention that an entrapment zone position in Suisun Bay favors delta smelt, but the reason for this effect is not well understood. (O28)

Biological Interactions (X-AB24-28)

119 Biological interactions in the entrapment zone are based primarily on potential species interactions inferred from life history, stomach content analyses, and laboratory feeding studies. Few biological effects are known from field studies in the entrapment zone. It is assumed that entrapment zone populations are regulated, in part, by predation mortality and competition for limited resources, such as food or space. We speculate that the entrapment zone's hydraulically concentrated food supply would reduce the biological effects related to resource competition, but could increase predation mortality through a "watering hole" effect.

120 Biological effects from the introduction of *Potamocorbula* have been detected by the long-term monitoring programs. The clam occupied bottom space to the exclusion of other benthic species, as measured by reductions in their average densities. The increased density of the clam in Suisun Bay has been correlated with declines in concentrations of phytoplankton, which has had repercussions through the food chain. Anecdotal information suggests that the clam has become a popular prey item for demersal fish, such as sturgeon and rays. The degree to which entrapment zone conditions have enhanced or diminished the clam's biological effects cannot be discerned from the available number of sampling sites in and out of the entrapment zone.

121 Egg ratio data and feeding experiments have revealed that *Eurytemora affinis* is not often food-limited in the entrapment zone. Thus, the tenfold decline in abundance that occurred upon the spread of *Potamocorbula* is believed to have been due to direct predation on nauplii. The same cannot be said for *Neomysis*, which declined as well, but which has no life stages small enough to be vulnerable to ingestion by clams. Therefore, at least now *Neomysis* appears to be food limited, and there is some evidence that it has been food-limited in the past.

122 The influence of introduced copepods (*Sinocalanus* and *Pseudodiaptomus*) on extant species is still unknown, although each arrived at times of decline in abundance of *Eurytemora*. Neither of these introduced genera are known to be particularly carnivorous, suggesting competition as a mechanism for a negative effect, but this is not supported by experimental results, which did not show food limitation of *Eurytemora*.

123 *Eurytemora* may use other food sources than phytoplankton, such as microzooplankton or detritus. This raises the possibility that *Eurytemora* depends ultimately on exogenous sources of carbon for its nutrition.

124 Striped bass larvae may also be food limited in and near the entrapment zone, even though they are not starving. Recent changes in the food web in the entrapment zone have resulted in a shift in the diet of young bass toward more benthic prey, but the overall availability of food may not have decreased very much. Growth rates, which are primarily dependent on feeding, are variable from year to year, possibly because of food limitation; however, rice pesticides may have affected growth before 1991. The abundance of food in the entrapment zone is considerably lower than in other estuaries where striped bass rear, and where food limitation has been observed. Experimental evidence supports the theory that slow-growing (and therefore small) larvae are more vulnerable to predation, and that therefore the rate of growth should be inversely related to survival.

DOWNSTREAM

125 This conceptual model refers to the region downstream of the entrapment zone, as far down as the Golden Gate. The South Bay is mostly excluded, since a lot of this area is out of the range of IEP sampling. However, the extensive knowledge of South Bay from USGS research is used here to make inferences about the rest of the downstream area.

126 In general, the downstream region appears to be less under the control of hydrodynamics than the upstream or entrapment zone regions. Freshwater and tidal flows exert a strong influence even in this region, but biological controls may be relatively more important. However, there is little information on which to base this opinion. Oceanic conditions may be important here, especially in affecting the abundance of larvae available for recruitment to bay populations.

Direct Environmental Effects

127 **Freshwater flow** has only indirect effects on biota in the downstream region. There is good evidence of net estuarine circulation, with net inward flow near the bottom and outward flow near the surface. Stratification is common in the channels, particularly on ebb tides, and is apparently influenced by freshwater flow. (A14, 15, 18)

128 Freshwater outflow has a strong influence on the longitudinal salinity gradient in the downstream area. There is a nearly linear response of the longitudinal position of a given bottom salinity and the log of net delta outflow. This relationship may be obscured in the vicinity of some of the rivers (e.g. Napa, Petaluma) during runoff events. (A15)

129 Outflow has considerable effect on residence time of San Francisco Bay and therefore on exchange with the ocean, but a quantitative understanding of this is lacking. Exchange between the shallow bays and the deeper channels is poorly understood, and may be affected by outflow to some degree. Fresh water entering the bay brings nutrients and can reduce transparency through transport of suspended matter. Presumably fresh water brings exogenous carbon downstream, but the extent and importance of that are unknown. (A18, 19, 21-23)

130 **Ocean conditions** (i.e. sea level) affect circulation through influences on tidal stage. Ekman transport away from the coast, caused by the northwest winds predominant in summer, lowers sea level. Southerly winds cause onshore transport, raising sea level. Low atmospheric pressure along the coast also results in increases of sea surface elevation. Low-frequency changes in sea surface elevation result in exchange between bay and ocean, which is not well understood. These events are also coupled with changes in the temperature, salinity, and nutrient and organic matter content of coastal water. Salinity probably has little influence, but temperature in the ocean moderates fluctuations in the central bay. (D11, 18, 21, 22)

Tidal forcing causes most of the exchange between bay and ocean. It has major effects in setting up stratification and resuspending sediments, as well as short-term effects on the longitudinal salt distribution. (E14, 15, 18, 20)

Dredging Effects of dredging in the downstream area may differ from those elsewhere because of the extent of industrial activity and therefore contaminated sediments. In addition, all of the in-bay disposal sites are in this area. No biological effects of dredging or disposal have been demonstrated other than obvious ones such as removal or inundation of benthic fauna. (G9, 27)

Exchange with the ocean may provide either a source or sink for organic matter and nutrients in San Francisco Bay. The highly productive upwelling region supplies a substantial fraction of the organic matter oxidized in Tomales Bay in summer; the rate of supply may actually be higher in San Francisco Bay because of the stronger estuarine circulation. However, the rate of export appears also to be high. The central bay appears to be a net consumer of organic matter, in that longitudinal profiles of inorganic nutrients often show a "hump" in the higher-salinity regions of the bay. The distribution of sources of this organic matter is unknown. (R21, 22)

Biological Responses to Environment

131 **Phytoplankton** and benthic microalgae produce most of the organic carbon in the downstream region. The relative importance of benthic microalgae is unknown, but based on a few measurements, microalgae could be as productive as phytoplankton.

132 In the South Bay, a predictable spring bloom of phytoplankton occurs when stratification is induced by a combination of freshwater flow, input of solar heat, and a reduction in tidal energy during neap tides. The bloom occurs because stratification isolates phytoplankton above the critical depth, resulting in an excess of production over respiration averaged through the mixed layer, and insulating the phytoplankton from benthic grazers. In addition, the stability of the surface layer causes particles to settle out, increasing water clarity and therefore productivity. This mechanism may also operate in the northern reach downstream of the entrapment zone. Thus, benthic grazing may exert a controlling influence on phytoplankton biomass throughout the bay, particularly since the spread of *Potamocorbula amurensis*. (N, W24)

133 **Zooplankton** of the downstream area comprise several species of copepods and meroplankton. In addition, zooplankton species from neritic waters outside the Golden Gate are common, especially in central bay. Relatively few species are abundant in this region. Although salinity stress is usually given as the reason for this characteristic of estuaries in general, the cause is probably the high rates of selective predation in estuaries. *Acartia* is probably the most important genus in the bay below the entrapment zone in terms of biomass and transfer of energy to fish. Additional important species are one or more *Oithona* species, and possibly the pelagic harpacticoid *Euterpina acutifrons*. (N26)

134 Direct physical effects on these species are probably limited to those due to stratification and to tidal exchange and export to the ocean. Losses to the ocean would be mainly tidally-driven, although residual gravitational circulation would favor retention or inward movement of species that remain near the bottom. Since *Acartia* species tend (in general) to avoid the surface layers and are capable of tidally-oriented vertical migration, this may not be an issue. If that is true, the residence time in the bay for these copepods would be much longer than typical population turnover times, so biological interactions would be more important than physical factors in this region. (N, R26)

135 **Benthos** The benthos of much of the downstream area has become dominated by *Potamocorbula*. The routine IEP sampling conducted downstream of the entrapment zone shows depression of chlorophyll and copepod abundance, but this sampling extends only as far as Carquinez Strait or San Pablo Bay.

136 Presumably recruitment of benthic species in this region would be strongly physically controlled as it is elsewhere. Controls would include the strength of tidal currents and gravitational circulation; probably most benthic species have larval stages that can use circulation patterns to arrive at habitat suitable for settling. Several benthic species have pelagic larvae that must recruit from the coastal ocean. (N, R27)

137 **Fish** Ocean conditions and position of the salt field influence fish in the downstream area. Marine species are prevented from going far upstream by low salinity, so the amount of habitat varies inversely with outflow. (D, O28)

138 Fish species in this region include starry flounder, English sole, Pacific herring, northern anchovy, staghorn sculpin, and plainfin midshipman. Several of these are estuarine-dependent. Some estuarine resident species may have larval stages that use flow patterns to enter the estuary, or to move downstream in the case of anadromous species, but little is known of this.

Biological Interactions (X-AB24-28)

139 Most of the limited knowledge of biological interactions in the downstream area comes from studies in the south bay. Cloern and others have made a convincing case that phytoplankton production and biomass are limited most of the time by benthic grazing. This limitation may carry over to higher trophic levels: egg production of the copepod *Acartia* sp. increases during the spring bloom, and bacterial biomass responds strongly to the bloom.

140 Upon introduction of *Potamocorbula amurensis*, abundance of *Acartia* spp. declined precipitously, as did *Eurytemora* in the entrapment zone. It is unclear whether *Acartia* declined because of predation, food limitation, or both, although the clams can consume the nauplii of *Acartia* as they can those of *Eurytemora*. In addition, the harpacticoid copepod *Euterpina acutifrons*, which is resistant to clam predation, appears to be very abundant, which it was not in previous years.

141 Feeding by fish is least well known in this region. Little is known of the early life history of fish in this region of the estuary.

Part II
INFORMATION NEEDS

This section presents the needs for information on the estuary that arise from consideration of the gaps identified in the conceptual models. Filling these gaps would provide better understanding of the functioning of the ecosystem. However, not all of the gaps have implications for management of the estuary or its watershed. For the purposes of planning IEP investigations, the utility of the results to management must be considered and explicitly stated. Management aspects of the information gaps are considered in prioritizing questions outlined below.

Management concerns can be listed in the following general categories:

- Effects of freshwater flow and diversions on the estuarine ecosystem.
- Long-term patterns of abundance or biomass and causes for any changes.
- Effects of other factors on the estuarine system that are indirectly related to flow (e.g. toxic materials from agricultural drainage).
- Effects of anthropogenic factors unrelated to flow that might confound relationships of ecosystem components to flow (e.g. effect of sewage-derived nutrients or organic matter, introduced species).
- Effects of natural or uncontrollable factors that cause variation in the ecosystem (e.g. climate).

These management concerns are particularly important in dealing with special-status species and particularly valued habitats. Management concerns were used in prioritizing information needs.

The information needs are posed as questions that could be answered by a combination of monitoring, modeling, and applied research. Each of the important questions is accompanied by some explanatory text. In addition, cross-references are made to the matrices and to Part I of the conceptual model by paragraph number to allow for easy reference to claims about the importance and significance of each question.

The basic criterion used to identify questions with high priority was that they address significant gaps identified in the conceptual models and matrices, and that these gaps are related to one or more of the management criteria listed above. Thus, the answers to high-priority questions would provide improved understanding that would benefit management of the estuary.

The underlying purpose of the matrices was to highlight important areas of ignorance. The areas identified on the matrices by large, dark markers should receive close attention. These fall into the following general categories:

- The mechanisms behind many of the effects of flow on the biota.
- The role of behavior and residence time in maintaining organisms in various parts of the estuary.
- The factors that influence the success and effects of introduced species.
- The effects of toxicants on populations.
- Biological interactions (predation, competition) in any part of the estuary.
- The role of benthic microalgae, microbenthos, and microzooplankton in the ecosystem.

Many of these questions are broad and pertain to numerous components of the ecosystem. Thus, these questions would require an interdisciplinary approach. They could form the basis for long-term programs of studies integrated with ongoing monitoring efforts.

The questions are divided into three sections:

- High-priority questions directly addressing serious gaps in knowledge.
- Lower-priority questions that either address gaps of lesser importance, or follow up the high-priority questions.
- Questions that are largely theoretical or not addressable by usual modes of scientific inquiry.

HIGH-PRIORITY QUESTIONS

Circulation and Transport

1 What are the tidal and residual flow patterns in the estuary?

Direct effects, all sections; Matrices: A-F 16-18, P-R 24-28.

Calibration and validation of hydrodynamic and particle tracking models depend on the availability of flow data from key locations in the system. Examples of gaps in knowledge of these flows are: the direction and magnitude of net flows between the lower San Joaquin River and the Sacramento via connector channels; and the direction and strength of net circulation cells in Suisun Bay. In addition, there is little knowledge of the evolution of vertical mixing in channels and between channels and shoals through the spring/neap cycle and as flow changes.

2 How do advection and dispersion move particles of different characteristics through the estuary?

67, 68, 71, 98; Matrices A-F 20,22-28.

Especially in the delta, the relative importance of dispersion and advection are poorly understood. Although knowledge is improving in this area by the development of particle tracking models and the use of advanced instrumentation, a lot more needs to be learned that is fundamental to understanding the ecology of these regions. The particle tracking models need to be validated, and the behavior of living "particles" needs to be determined so their movement can be modeled effectively.

3 How is the residence time of water or particles in any given area affected by:

- Tidal advection?
- Dispersion?
- Freshwater flow?
- Export pumping?
- Lateral circulation?
- Bathymetry and channel geometry?

28-32, 71, 101, 129; Matrices: A-G 16-19

This is related to the previous question. Residence time is the inverse of exchange rate, and residence time of particles can be quite different from that of water. The various forcing functions work differently in different parts of the estuary. The relationships among these are understood conceptually, but not quantitatively, and the relative importance of the various forcing functions is unknown.

Effects of Flow Patterns on Biota

4 What are the population-level implications of changes in survival of the species or life stages vulnerable to entrainment in export pumps?

12, 70, 83, 88; Matrices: C24-28

Despite a plethora of data on salvage losses of many fish species, there is little basis for determining whether these losses constitute a major source of mortality to these species. There is evidence to suggest that zooplankton entrainment has negligible effects on species of the entrapment zone and even upstream.

5 What are the population-level implications of changes in survival of the species or life stages vulnerable to entrainment in agricultural diversions in the delta?

11, 69; Matrices: B24-28

Net delta consumption is similar in magnitude to export flows in summer, and gross diversion flows must be much larger. Removal of fish and other biota must be important to at least some populations.

6 How do tidal and residual flow patterns interact with behavioral patterns of resident species to regulate retention?

110, 117; Matrices: E24-28

It is believed, based on limited data from this estuary, that many species of plankton and fish adjust their vertical position to affect their horizontal movement, thereby retaining the population within the estuary. Only this year have measurements been made of vertical position and flow velocities.

7 What are the effects of advection, tidal dispersion, and residence time on the maintenance of populations and in larval recruitment of fish and invertebrates?

82, 88, 108, 116; Matrices P-S 24-28.

This is related to the previous question. All populations throughout the estuary are subjected to various flows that would move them from their preferred or optimal habitat. Each population must respond either by developing behavioral mechanisms to effect retention, or by achieving a high enough reproductive and growth rate to overcome losses.

8 What mechanisms (direct or indirect) cause covariation of the abundance of bay resident species with delta outflow or X_2?

51, 88, 89, 118; Matrices A26-28 (Indirect).

This covariation has been observed for species with a wide variety of habitats and life histories, implying an underlying mechanism. However, the mechanisms for each species could differ. If protective measures are to be successful, it is essential to understand these mechanisms, including the habitat requirements of the species of concern.

9 What effect does exchange between channels and shoals have on phytoplankton, zooplankton, larval fish, and benthos?

41, 78, 108, 112, 132; Matrices P, Q, S24, 26-28.

The conceptual model for phytoplankton in the entrapment zone indicates the importance of shoals for maintaining high production and biomass, but this effect has not been demonstrated for other parts of the estuary or other trophic levels. This could be very important for fish.

10 How does the behavior of Chinook salmon and juvenile striped bass affect their distribution, passage, and survival through the delta?

88, 89; Matrices A, B28 (Direct and indirect).

11 How is recruitment of bay resident species affected by exchange with the ocean?

133, 134, 136, 138; Matrices R26-28.

Many estuarine resident species have larvae that leave the estuary and reside in the ocean before settlement back in the estuary. Examples abound in the literature of larvae of benthic or fish species that find their way back into an estuary to recruit. Freshwater outflow could have major indirect effects on recruitment through regulation of net inflow at the bottom.

Trophic Interactions

12 What are the roles of various sources of organic matter in providing energy to higher trophic levels?

35; Matrices V, X25-28.

The traditional view of the food web describes it as a linear chain from phytoplankton to zooplankton to fish. This is an outmoded view: other sources of energy are more important than phytoplankton, especially in the upper estuary. If that is true, then the mechanisms for control of abundance of the higher trophic levels need to be reconsidered.

13 What are the feeding relationships among important native and introduced species and their food sources within the bay and delta including:

- Phytoplankton,
- Detrital organic carbon,
- Bacteria,
- Microzooplankton,
- Zooplankton (with emphasis on the relationships among native and introduced species),
- Benthos (with emphasis on recent introductions such as *Potamocorbula* and *Gammarus*),
- Fish.

All Biological Interactions sections; Matrices J, X-AB24-28.

Additional work needs to be done on the feeding relationships within the estuary so that a general, quantitative description can be made of feeding relationships among all major species. Such a description would be very useful in determining pathways for indirect influences such as toxicants or species introductions.

Regulation of Populations

14 How are populations of fish in the bay and delta regulated? What is the importance of:

- Habitat characteristics,
- Flow patterns,
- Export losses,
- Recruitment,
- Feeding and food supply in early life,
- Predation,
- Density-dependent mechanisms.

All Biological Responses and Biological Interactions sections; Matrices A-C28, X-AB28.

This question is really fundamental to managing fish populations; by the same token it is extremely general and would require a tremendous effort to answer for even one fish population. Nevertheless, answers to some of these questions would enable managers to target the most sensitive life stages for management activity, thereby possibly reducing the necessity for broad-scale activities such as season-long increases in flow.

15 How are populations of zooplankton, microzooplankton, phytoplankton, and benthos regulated, by the same factors as above?

All Biological Responses and Biological Interactions sections; Matrices A-C24-27, X-AB24-27.

If fish populations are limited by recruitment, then the food source for young stages needs to be considered. Also, these groups have their own responses to changes in freshwater flow and other management actions, and these responses also need to be understood if an ecosystem view is to be taken.

16 What factors control the development and distribution of blooms of the nuisance alga *Melosira granulata*?

76-80; Matrices A, B, P, W24 (?).

Blooms of this alga in the delta may be occurring more frequently than in the past, yet the cause of these blooms is poorly understood. Determining causes of the blooms might enable managers to prevent blooms, thereby alleviating several environmental and economic problems.

17 How important are benthic microalgae in the carbon budget of the estuary?

131; Matrices W, X27.

Other Questions

18 What are the direct, population-level effects of toxicants on microzooplankton, zooplankton, benthos and fish? 19, 74; Matrices I24-28.

Numerous effects of toxicants have been inferred from body burdens or similar organismal evidence, or from results of histological sampling or toxicity bioassays. In no case have these effects been shown to cause a bay-wide reduction in population abundance or production. Although such a demonstration can be very difficult, it seems to be an essential part of the evaluation of the status of the estuary.

19 What is the diurnal difference in abundance, location, or vulnerability of major species in the bay and delta?

Matrices NA.

This is not covered directly in the matrix, but is important from a sampling perspective. Most of the sampling done in the estuary has taken place by day, with only a handful of nighttime samples having been taken. Yet, it is well known that many species of fish, zooplankton, and epibenthos redistribute themselves or become more vulnerable to sampling at night. Data on nighttime distributions would either give confidence that the daytime sampling has been effective for determining abundance, or would suggest that some of the abundance data be reconsidered. In addition, for species that feed at night, feeding relationships could differ substantially from those determined from daytime sampling.

LOWER-PRIORITY QUESTIONS

Effects of Flow and Other Environmental Conditions on Biota

20 Are species diversions proportional to the diversion flow rates?

21 What are the effects of other diversions such as for power plant and other industrial users, and Contra Costa Canal and North Bay Aqueduct?

22 How do behavior patterns governing the location of resident species vary with season, turbidity, water velocity, or size and motility of the organisms?

23 Are there flow regimes that reduce predation by *Potamocorbula*?

24 To what extent is there a counterpart in other areas to the predictable spring bloom of south bay?

25 How do changes in oceanic conditions (e.g. *El Niño*) affect the bay?

26 What factors are responsible for the continuing increase in water transparency throughout the estuary and what effect does this have on estuarine ecology?

Trophic Interactions

27 How do behavior patterns affect the amount of food actually available to a given species? How do these behaviors vary with season, age, or environmental conditions?

28 How do behavior patterns that govern the location of a given species of zooplankton or ichthyoplankton in the estuary vary with the presence of predators or the location or abundance of food?

29 How does the concentration of particles and organisms by the entrapment zone affect foraging behavior and success there relative to outside the entrapment zone (effects of elevated concentration as well as reduced visibility)?

30 Do *Melosira* blooms interfere with larval fish feeding, or decrease their encounter probability with potential predators?

Other Questions

31 What are the trophic pathways for persistent toxicants?

32 What can the identification of sublethal exposures (e.g. affected livers in striped bass larvae) tell us about the overall impact of toxicants?

33 Have toxicants disproportionately affected native fishes that spawn in shallow upstream habitats (e.g. smelt and splittail)?

THEORETICAL QUESTIONS

Although these questions do not lend themselves to the selection of a methodology for answering them, they are of great interest for heuristic purposes. Scientists working in various aspects of the ecosystem might keep these questions in mind when formulating monitoring and research plans.

34 Is it feasible to construct one or more ecosystem models for the estuary?

The Central Valley Project Improvement Act calls for the use of ecosystem models to address the impacts of the CVP on the ecosystem. Such models would be highly desirable for exploring system behavior and formulating hypotheses, as well as for management. However, there are no such models available. This is a theoretical question because the underlying causal mechanisms are unknown. For example, a model describing carbon flow in the estuary, a common form of ecosystem models, could not be completed for this estuary without considerably more detail on the sources and fates of organic matter. Similarly, a model of population dynamics of any species cannot be constructed until better information is available on the important regulatory mechanisms in the population.

35 Must we study the impacts of exotic species on a case-by-case basis, or are there inherent features of this estuarine food web that allow an understanding of how introductions will succeed, and how they will shape the food web?

This question is more theoretical than answerable by a program of field work, but is worth posing and considering since future introductions are practically guaranteed. In addition, this question is of great ecological interest, and the success of introductions may tell us something about the vulnerability or resilience of ecosystems, or the virulence of invading species, in general.

36 What can we do to prepare for possible future changes in the estuary, such as:

- Global warming and sea level rise,
- Subsidence of delta islands and collapse of levees,
- Increasing urbanization,
- Additional catastrophic introductions (e.g. zebra mussel)?

Some changes are inevitable, and others are probable. Being prepared for these changes could make them less painful when they arrive.

37 What are the desirable characteristics of the estuary, and in what order of priority should these be maintained?

This is a societal question, not a scientific one. That is, society as a whole must decide how to balance the competing uses of water, and the importance of various attributes of the estuary. This is being done now through a combination of economic forces and regulatory actions, the most important current one being the Endangered Species Act. Is there a more rational way to do this?

COMMON ABBREVIATIONS AND METRIC CONVERSIONS

Area

km^2	square kilometers; to convert to square miles, multiply by 0.3861
m^2	square meters; to convert to square feet, multiply by 10.764

Length

cm	centimeters; to convert to inches, multiply by 0.3937
FL	fork length; length from the most anterior part of a fish to the median caudal fin rays (fork in the tail)
km	kilometers; to convert to miles, multiply by 0.62139
m	meters; to convert to feet, multiply by 3.2808
mm	millimeters; to convert to inches, multiply by 0.03937
SL	standard length; tip of upper jaw of a fish to crease formed when tail is bent sharply upward
TL	total length; length from the most anterior part of a fish to the end of the tail

Volume

AF	acre-foot; equal to 43,560 cubic feet
L	liters; to convert to quarts, multiply by 1.05668; to convert to gallons, multiply by 0.26417
mL	milliliters

Flow

cfs	cubic feet per second; to convert to acre-feet per day, multiply by 1.98
gpm	gallons per minute
mgd	million gallons per day

Velocity

fps	feet per second
m/s	meters per second; to convert to feet per second, multiply by 3.2808

Mass

kg	kilograms; to convert to pounds, multiply by 2.2046

Concentration

mg/L	milligrams per liter; equals parts per million (ppm)
µg/L	micrograms per liter; equals parts per billion (ppb)

Specific Conductance

µS	microsiemens; equivalent to micromhos
µS/cm	microsiemens per centimeter

Temperature

°C	degrees Celsius; to convert to °F, multiply by 1.8 then add 32 degrees
°F	degrees Fahrenheit; to convert to °C, subtract 32 degrees then divide by 1.8

Mathematics and Statistics

df	degrees of freedom
e	base of natural logarithm
E	expected value
log	logarithm
N	sample size
NS	not significant
%	percent
‰	per thousand
P	probability
r	correlation or regression coefficient (simple)
R	correlation or regression coefficient (multiple)
SD	standard deviation
SE	standard error
V	variance

Interagency Program Members

COE	U.S. Army Corps of Engineers
DFG	California Department of Fish and Game
DWR	California Department of Water Resources
EPA	U.S. Environmental Protection Agency
FWS	U.S. Fish and Wildlife Service
NMFS	National Marine Fisheries Service
SWRCB	California State Water Resources Control Board
USBR	U.S. Bureau of Reclamation
USGS	U.S. Geological Survey

General

CPUE	catch per unit effort
YOY	young of the year

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